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RESEARCH ARTICLE

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Picea omorika (Pinaceae): an endangered endemic species from Serbia and Bosnia-Herzegovina, locally naturalised in the Brembana Valley (Orobic Alps, Italy)

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Abstract

Picea omorika is an endangered conifer endemic to Serbia and Bosnia-Herzegovina. This research reports the first case of its naturalisation in Italy, specifically in a restricted area of the upper Brembana Valley (Orobic Alps, Lombardy), where an uneven-aged population, of approximately 50–60 individuals, grows within a wood pasture at 1,760–1,790 m a.s.l., inside the Orobie Bergamasche Regional Park. Dendrochronological analysis indicates that this population likely originated from a single tree planted for ornamental purposes near a mountain hut in the 1960s. Over the past 30 years, the species has propagated in the study area under cold, suboceanic climatic conditions and on moderately moist, nutrient-poor, slightly acidic soils, as inferred from climatic data and Ellenberg ecological indicator values. Grime's competitor, stress tolerator, ruderal (CSR) functional strategy analysis classified *P. omorika* as a strictly stress-tolerant species (C = 0.0%, S = 100.0%, R = 0.0%) with low invasive potential. Phytosociological analysis indicates that the *P. omorika* community is part of a secondary succession that is progressing from pastures of *Nardion strictae* towards high-montane coniferous forests of *Piceion excelsae*. This research contributes to a better definition of the ecological niche of *P. omorika*.

Keywords

Alien species, CSR functional strategy, Ellenberg indicator values, naturalisation, serbian spruce, southern Alps

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Introduction

Picea omorika (Pančić) Purk., commonly known as the Serbian spruce, is a conifer endemic to a restricted mountain area along the middle course of the Drina River, between western Serbia and eastern Bosnia-Herzegovina, within an area of approximately 10,000 km^2 (Mataruga et al. 2020; Vacek and Vacek 2023). In its natural range, it grows on steep slopes and on soils with diverse physico-chemical properties (Savill et al. 2017), at elevations between 800 and 1,700 m a.s.l., forming mixed forests of *Erico carneae-Piceion omorikae* Mucina & Čarni, 2016 phytosociological alliance (Mucina et al. 2016), characterised by a set of species such as *Epipogium aphyllum* Sw., *Equisetum hyemale* L., *Euphorbia glareosa* Pall. ex M.Bieb., *Anthoxanthum australe* (Schrad.) Veldkamp, *Petasites kablikianus* Tausch ex Bercht., and *Saxifraga tridactylites* L. (Ilić et al. 2022).

Over the past decades, several studies have investigated the genetic, morpho-anatomical and phytochemical variability of *P. omorika* populations from Serbia and Bosnia-Herzegovina, highlighting differences between Serbian and Bosnian populations in terms of needle morphology, leaf anatomy and phytochemical composition (Nikolić et al. 2023, 2024, 2025). Recently, Tichý et al. (2023) provided Ellenberg ecological indicator values for *P. omorika*, contributing to filling a gap in the ecological characterisation of the species; nonetheless, its position within the competitor, stress tolerator, ruderal (CSR) framework proposed by Grime (2001) has not yet been determined.

Palynological and palaeobotanical evidence indicates that during the Tertiary period, a species of the *Picea* genus (*P. omorikoides* C.A.Weber), sharing similar traits with *P. omorika*, was widespread across large areas of central and southern Europe, including the Alps (Ravazzi 2002). However, climatic oscillations during the glacial and post-glacial periods led to its disappearance from the Alps, probably as a consequence of the reduction of suitable habitats and increased competition with more adaptable conifer species (Ravazzi 2002).

The current fragmentation of the distribution range and the low connectivity among *P. omorika* populations have raised concerns regarding the species' genetic diversity and natural regeneration capacity in Serbia and Bosnia-Herzegovina (EUFORGEN 2024). Furthermore, due to its extremely restricted distribution, competition with other forest species (particularly broadleaf trees; Savill et al. 2017) and high vulnerability to climate change, *P. omorika* has been classified as "Endangered" on the IUCN Red List (Aleksić et al. 2017). The conservation of this species is, therefore, considered a priority, owing to both its ecological value and its phylogenetic significance as a glacial relict. Consequently, *P. omorika* is legally protected in both Serbia and Bosnia-Herzegovina. In Serbia, all individuals of *P. omorika* are protected, with the main populations included within Tara National Park, whereas in Bosnia-Herzegovina the species is listed among those whose felling, uprooting, or damaging is prohibited under forestry and protected-area legislation (Mataruga et al. 2020).

In modern times, *P. omorika* has been widely cultivated for ornamental purposes, owing to its slender columnar habit, the silvery sheen of the needle undersides, and its tolerance of a broad range of edaphic and climatic conditions (Savill et al. 2017; Vacek and Vacek 2023). Although planted in numerous gardens and parks across Europe,

no stable cases of naturalisation have been documented outside its native range so far (Vacek and Vacek 2023; EUFORGEN 2024). This suggests that the species depends on highly specific ecological conditions to complete its full life cycle, thereby rendering its long-term conservation in (semi-) natural habitats challenging.

This research aims to report the first case of a local naturalisation of *P. omorika* in Italy (Brembana Valley, Orobic Alps). In addition, it seeks to elucidate the potential causes of its introduction, assess its CSR functional strategy, and analyse the ecological and phytosociological features of the plant community in which it occurs, thereby enhancing current knowledge of the environmental conditions suitable for the establishment/conservation of this species.

Occurrence and study area

The *P. omorika* stand is located within the municipality of Carona (Province of Bergamo, administrative region of Lombardy), in the upper Brembana Valley (WGS84: 46.028056°N, 9.860556°E), at an elevation between 1,760 and 1,790 m a.s.l. (Fig. 1). The site lies within the boundaries of the Orobie Bergamasche Regional Park and is characterised by a suboceanic pre-Alpine climate, with abundant annual precipitation (> 1,700 mm) mainly distributed during the equinoctial periods and summer months (Fig. 2).

The soil in the study area is a podzol developed on acidic rocks belonging to the Collio geological formation (Lower Permian) (Provincia di Bergamo 2002). From a geobotanical perspective, the area falls within the South-Orobic District (Andreis 2002), which is characterised by a high number of endemic species (Martini et al. 2012), including some acidophilous species typical of the montane and subalpine vegetation belts such as *Sanguisorba dodecandra* Moretti and *Viola comollia* Massara (Bertolli 2024). The current potential vegetation is the Norway spruce forest of the *Vaccinio-Abietenion* Oberd., 1962 suballiance (alliance: *Piceion excelsae* Pawłowski et al., 1928), which is widespread in Lombardy in the high montane and subalpine belts of the mesalpic region, including the Orobic Alps (Del Favero 2002; Andreis et al. 2009). The secondary succession leading to this forest type (*Luzulo niveae-Piceo excelsae* sigmetum) generally starts from *Nardion strictae* Br.-Bl., 1926 pastures (Verde et al. 2010).

Within the study area, approximately 50–60 Serbian spruces of various sizes were counted (Fig. 3). A more precise survey was not possible in some inaccessible areas with overhanging rocks and trees. These individuals are distributed across a wood pasture of about 1 ha. At the margin of this wood pasture, along the right bank of the Brembo stream, stands the Armentarga hut (Fig. 1), a small building constructed in 1950 to host workers involved in building the artificial dam of Lake Fregabolgia for hydroelectric power production. In 1952, the hut was acquired, renovated, and has since been managed as a private alpine refuge by the "Penne Nere" Alpine Group of Bergamo.

Until the mid-20th century, the area was used for summer grazing of livestock, mainly cattle and sheep (personal communication). Since the 1950s, the abandonment of traditional pastoral activities has driven gradual forest expansion and the formation of a wood pasture, resulting in the current mosaic of open areas and tree stands. Within

Figure 1. Distribution of *Picea omorika* in Europe (data source: GBIF database) and location of the new occurrence in Italy. The study area (wood pasture with *P. omorika*) is highlighted in green.

this context, a single Serbian spruce grows in proximity of the Armentarga hut (Fig. 4), whereas all other individuals occur at least 10 m away in areas that were still open pastures in the 1950s and have since evolved into wood pasture (Figs 1, 3a), reflecting the land-use change that has occurred throughout the Alpine chain since the second half of the 20th century (Cislaghi et al. 2019). No forest plantations or reforestation activities involving *P. omorika* have been carried out in t he study area over the past century, as confirmed by data from the technical-environmental offices of the "Comunità Montana Valle Brembana" (Protocol No. 6062/11/2/AG/mb) and the Municipality of Carona (personal communication).

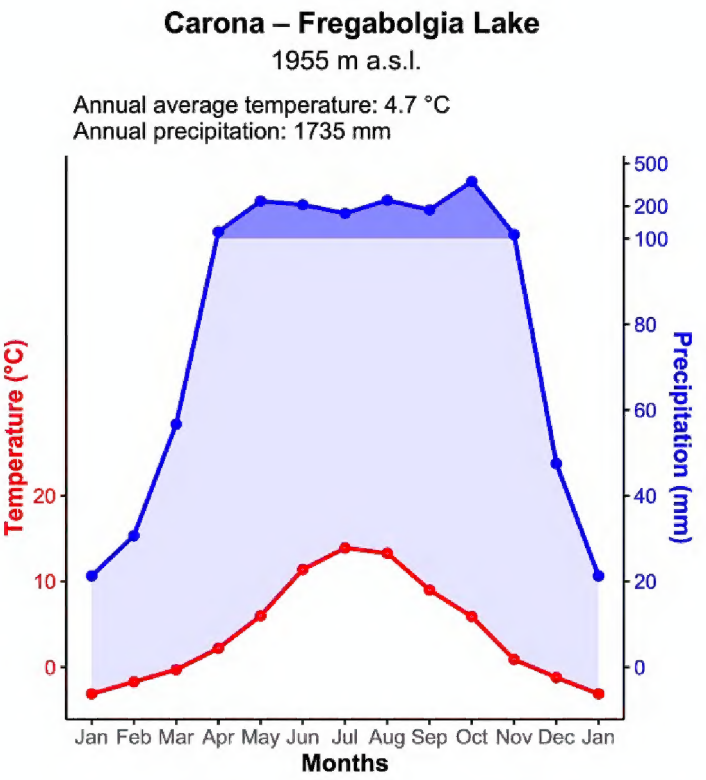

Figure 2. Ombrothermic diagram of the weather station of Lake Fregabolgia (Carona - BG, WGS84: 46.024167°N, 9.861944°E). Data source: ARPA Lombardia (2015–2024).

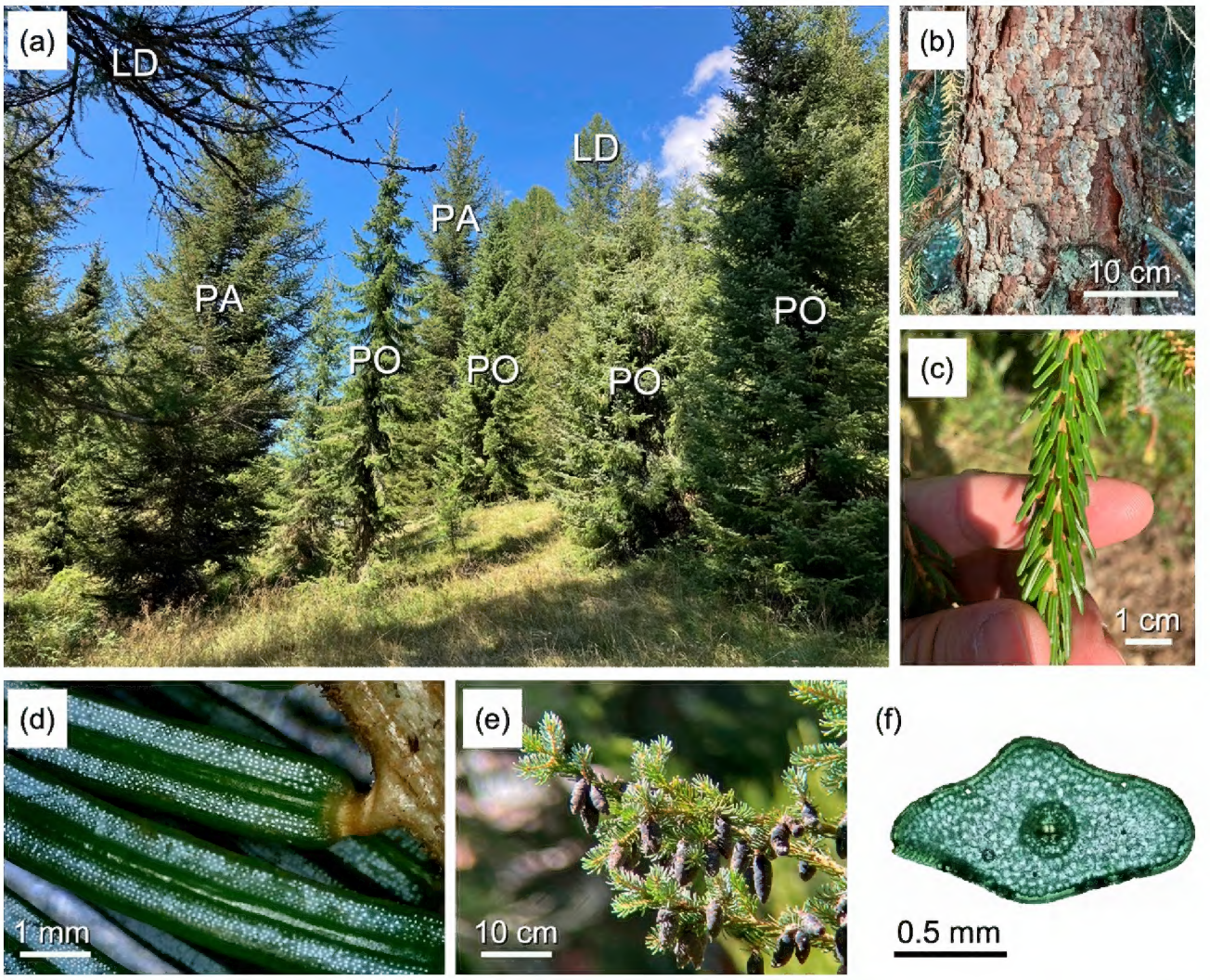

Figure 3. Morphological characteristics of *Picea omorika* growing in the study area. **a** general view of the stand showing *P. omorika* (PO) surrounded by *P. abies* (PA) and *Larix decidua* (LD) **b** bark of *P. omorika*, showing thin, scaly plates with reddish-brown tones **c** shoot with slender, keeled needles, 0.8–1.8 cm long and 1.1–1.8 mm wide **d** needle underside with two broad white stomatal bands composed of 4–6 lines each. **e** female cones at the upper part of the crown; they are pendulous, resinous, dark bluish-violet, ovoid to oblong, and reach up to 6.5 cm in length when mature **f** microscopic section of a needle showing its bilaterally flattened shape.

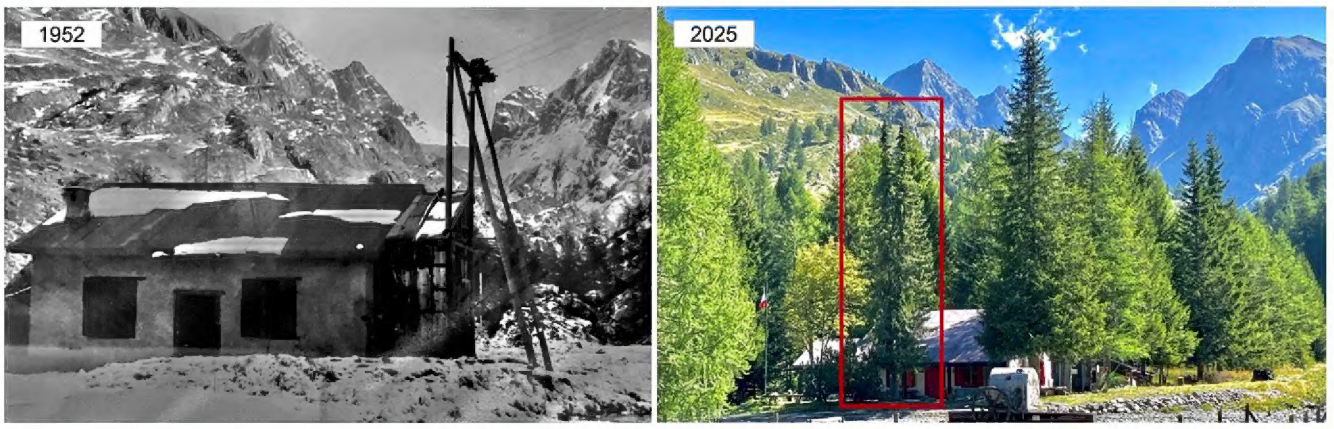

Figure 4. The Armentarga hut in 1952 (photo from the archive of the "Penne Nere" Alpine Group) and in 2025 (photo by Giupponi L.). The red box marks the Serbian spruce located near the hut, currently surrounded by Norway spruces and larches that were not present in 1952.

Materials and methods

Dendrochronological analysis

The age and growth dynamics of the *P. omorika* stand were assessed on a sample of 12 trees, selected to include individuals of varying heights and sizes to be as representative as possible of the stand. The sample also included the only Serbian spruce growing near the Armentarga hut.

Wood cores were collected from each tree at breast height (1.3 m above ground level) using a Pressler increment borer, and stem circumference at breast height (CBH) was measured with a tape measure. In the laboratory, the cores were examined under a stereomicroscope, and annual growth rings were counted to determine the age of each tree. Based on these data, the age of the sampled trees was established, and a growth model of stem circumference over time was developed. The model was constructed using linear regression analysis in the R environment (R Core Team 2025).

Vegetation data collection and analysis

In the study site, three phytosociological relevés were carried out over an area of 100 m^2 (10 × 10 m) following the classical Zürich-Montpellier school approach (Braun-Blanquet 1964). For each relevé, topographic data (elevation, aspect, and slope angle) were recorded, and total cover of trees, shrubs, herbaceous vegetation, and litter was estimated. The vascular plants were identified using the dichotomous keys of Pignatti et al. (2017–2019) and a cover-abundance index was assigned for each plant species according to the Braun-Blanquet scale: r = rare species in the relevé; + = cover < 1%; 1 = cover 1–5%; 2 = cover 5–25%; 3 = cover 25–50%; 4 = cover 50–75%; 5 = cover 75–100%.

Picea omorika was identified using the dichotomous keys of Do Amaral Franco (1993) and the morphological descriptions reported in the literature (Ballian et al. 2016; Savill et al. 2017; Vacek and Vacek 2023; Nikolić et al. 2025). A specimen was collected and deposited at the herbarium of the Museo di Storia Naturale di Milano (MSNM).

For the phytosociological analysis of the *P. omorika* community in the study area, various bibliographic sources were consulted (Aeschimann et al. 2004; Ubaldi 2008a, 2008b; Andreis et al. 2009; Landolt et al. 2010) as well as online portals, including "Prodromo della Vegetazione Italiana" (Biondi and Blasi 2014) and "FloraVeg.EU" (Chytrý et al. 2024).

The mean Ellenberg Indicator Values (EIVs), weighted by species cover, were calculated for each relevé in order to assess the ecological characteristics of the vegetation in the study area and compare these values with those recently assigned to *P. omorika* (Tichý et al. 2023). This study used the EIVs recently updated and extended for the entire European vascular flora by Tichý et al. (2023): light (L), temperature (T), soil moisture (M), soil reaction (R), nutrients (N), and salinity (S). The mean EIV values were calculated after transforming the Braun-Blanquet cover-abundance indices according to the ordinal scale proposed by van der Maarel (1979): r = 1; + = 2; 1 = 3; 2 = 5; 3 = 7; 4 = 8; 5 = 9.

The scientific names of the species follow version 2025.1 of the Portal to the Flora of Italy (2025), while the names of syntaxa (from class to alliance level) are in accordance with Mucina et al. (2016).

Functional strategy evaluation

The CSR functional strategy of *P. omorika* was assessed following the procedure described by Pierce et al. (2017). In particular, 50 healthy leaves were collected from the lower branches (at least two years old) of 10 different individuals. All samples were wrapped in moist paper and stored at 4 °C for one night. Fresh weight of saturated leaves was determined using an analytical balance (Precisa XB 220A). Leaf area was obtained by scanning the samples with a digital scanner and processing the images with ImageJ (Schneider et al. 2012). Dry weight was measured after oven-drying the leaves at 105 °C for 24 h. CSR values and the functional strategy were calculated using the "StrateFy" spreadsheet (Pierce et al. 2017). In addition, both weighted (according to species cover values) and unweighted mean CSR strategies of the whole plant community were computed. For this purpose, CSR values of the species within the community were retrieved from the field-portable list of CSR strategies (Pierce et al. 2017). CSR values were then visualised in the ternary CSR graph using the "ggplot2" package of R, highlighting point/species density levels through kernel density analysis.

Results

Specimen

Italy, Lombardia, Carona (Bergamo), presso la Baita Armentarga [near the Armentarga hut on the right bank of the Brembo stream] (WGS84: 46.028056°N, 9.860556°E), pascolo arborato [wood pasture], 1765 m a.s.l., SE, 26 August 2025, *L. Giupponi* (MSNM barcodes MSNM54947, MSNM54948; Fig. 5). Naturalised alien species new for the flora of Italy (Lombardia).

Figure 5. Herbarium sheet of *Picea omorika* deposited at MSNM (barcode MSNM54948).

Stand age and growth

Dendrochronological analysis of Serbian spruces revealed that the wood pasture supports an uneven-aged stand, comprising both young individuals (only a few years old) and mature trees exceeding 30 years (Fig. 6). Fig. 6 illustrates the linear increase in CBH with tree age. The individual growing near the Armentarga hut was found to be the oldest (54 years at breast height), despite exhibiting a CBH value comparable to that of 30–35-year-old trees in the wood pasture (Fig. 6).

Plant community

In the study area, 58 plant species were identified (Table 1), 75% of which are perennial herbs (hemicryptophytes: 66%; geophytes: 10%), and the remaining species are trees (9%) and shrubs (15%). Most of the species are European montane species (orophytes); some are endemic to the Alps, including *Sanguisorba dodecandra*, which is endemic to the Orobic Alps. *P. omorika* was the only non-native species recorded.

The data reported in the phytosociological table of the relevés (Table 1) indicate that the *P. omorika* plant community is composed of species from different vegetation types and that secondary succession is occurring in the study area. In fact, alongside species of

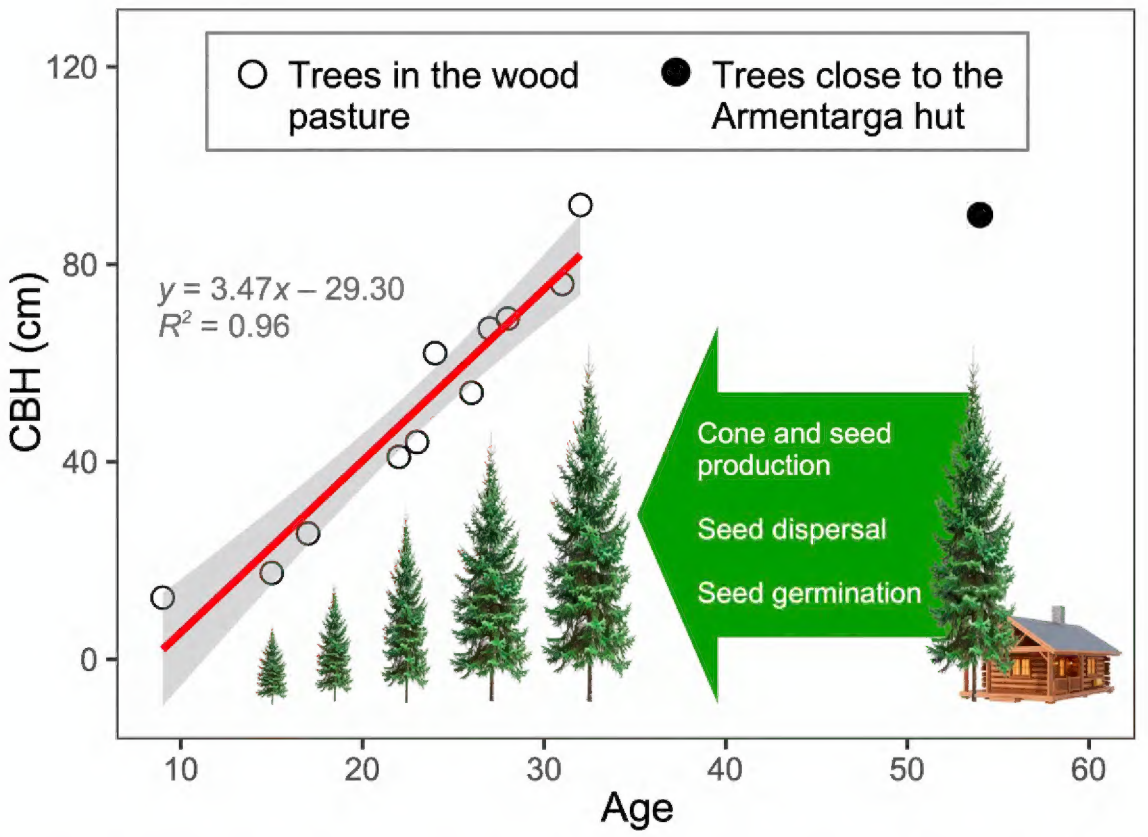

Figure 6. Relationship between tree age (years) and circumference at breast height (CBH). Open circles denote trees located within the wood pasture, whereas the filled circle represents a tree growing close to the Armentaraga hut. The red line indicates the fitted linear regression (based on open circles only), with the shaded area representing the 95% confidence interval. The regression equation and the coefficient of determination value (R^2) are also shown.

Table 1. Phytosociological table of relevés.

Biological Form	Chorological Type	**Relevé code**	**1**	**2**	**3**
		Area (m²)	**100**	**100**	**100**
		Slope (°)	**0**	**32**	**20**
		Aspect (°)	**-**	**157**	**127**
		Elevation (m a.s.l.)	**1780**	**1778**	**1770**
		Trees cover (%)	**40**	**70**	**30**
		Shrubs cover (%)	**5**	**50**	**25**
		Herbaceous cover (%)	**95**	**30**	**75**
		Litter cover (%)	**0**	**20**	**0**
		Number of species	**24**	**38**	**32**
		Target species			
P scap	Endem. W-Balkans	*Picea omorika* (Pančić) Purk.	1	2	2
		***Nardion strictae* Br.-Bl., 1926**			
H caesp	Circumbor.	*Agrostis capillaris* L.	1	1	2
H scap	Orof. SE-Europ.	*Centaurea nervosa* Willd. subsp. *nervosa*	+	+	1
H scap	Eurasiat.	*Potentilla erecta* (L.) Raeusch.	+	+	+
H caesp	Eurosib.	*Nardus stricta* L.	+	+	2
H scap	Endem. Alp.	*Campanula barbata* L.	.	r	r
H scap	Orof. SE-Europ.	*Campanula scheuchzeri* Vill. subsp. *scheuchzeri*	.	+	.
H ros	Centr.-Europ.	*Carlina acaulis* L. subsp. *acaulis*	.	+	.
H ros	Europ.-Caucas.	*Pilosella officinarum* F.W.Schultz & Sch.Bip.	.	+	.
H ros	Alp.-Piren.	*Plantago alpina* L.	.	.	+
		***Festucetalia spadiceae* Barbero, 1970 and *Juncetea trifidi* Hadac in Klika & Hadac, 1944**			
H scap	Alp.-Carpat.	*Carduus defloratus* L. subsp. *tridentinus* (Evers) Ladurner	.	+	+
H caesp	Endem. Alp.	*Festuca scabriculmis* (Hack.) K.Richt.	.	1	+
Ch suffr	Endem. Alp.	*Daphne striata* Tratt.	.	.	+
H scap	Orof. SE-Europ.	*Ranunculus montanus* Willd.	.	.	+
		***Molinio-Arrhenatheretea* Tx., 1937**			
H caesp	Subcosmop.	*Deschampsia cespitosa* (L.) Beauv. subsp. *cespitosa*	4	+	3
H scap	Eurosiber.	*Achillea millefolium* L. subsp. *millefolium*	.	+	1
H rept	Subcosmop.	*Trifolium repens* L.	.	+	+
G rhiz	Eurasiat.	*Bistorta officinalis* Delarbre	+	.	+
H scap	Subcosmop.	*Rumex acetosa* L. subsp. *acetosa*	+	.	.
H scap	Subcosmop.	*Silene vulgaris* (Moench) Garcke subsp. *vulgaris*	.	+	.
H caesp	Circumbor.	*Phleum alpinum* L.	.	.	+
		***Mulgedio-Aconitetea* Hadač & Klika in Klika & Hadač, 1944**			
H scap	Orof. Europ.	*Chaerophyllum hirsutum* L.	+	1	1
H scap	Endem. Ital.	*Sanguisorba dodecandra* Moretti	.	+	+
H scap	Eurasiat.	*Hypericum maculatum* Crantz subsp. *maculatum*	.	.	1
H scap	Alp.-Piren.	*Molopospermum peloponnesiacum* (L.) W.D.J.Koch subsp. *bauhinii* I.Ullmann	.	.	+
G rhiz	Eurasiat.	*Veratrum lobelianum* Bernh.	+	.	.
H ros	Subcosmop.	*Athyrium distentifolium* Tausch ex Opiz	+	.	.
H scap	Orof. Europ.	*Imperatoria ostruthium* L.	1	.	.
G rhiz	Orof. Centr.-Europ.	*Petasites albus* (L.) Gaertn.	+	.	.
G rhiz	Circumbor.	*Streptopus amplexifolius* (L.) DC.	r	.	.
G bulb	Eurasiat.	*Lilium martagon* L.	r	.	.
H scap	Circumbor.	*Chamaenerion angustifolium* (L.) Scop.	.	.	+

Biological Form	Chorological Type	Relevé code	1	2	3
		Area (m²)	**100**	**100**	**100**
		Slope (°)	**0**	**32**	**20**
		Aspect (°)	**-**	**157**	**127**
		Elevation (m a.s.l.)	**1780**	**1778**	**1770**
		Trees cover (%)	**40**	**70**	**30**
		Shrubs cover (%)	**5**	**50**	**25**
		Herbaceous cover (%)	**95**	**30**	**75**
		Litter cover (%)	**0**	**20**	**0**
		Number of species	**24**	**38**	**32**
		***Crataego-Prunetea* Tx., 1962**			
NP	Circumbor.	*Rubus idaeus* L. subsp. *idaeus*	1	2	2
P caesp	Orof. S-Europ.	*Laburnum alpinum* (Mill.) Bercht. & J.Presl	.	+	.
		***Vaccinio-Abietenion* Oberd., 1962 and *Piceion excelsae* Pawłowski et al., 1928**			
G rhiz	Circumbor.	*Phegopteris connectilis* (Michx.) Watt	+	.	.
H scap	Orof. SW-Europ.	*Astrantia minor* L.	+	.	.
H ros	Orof. Centr.-Europ.	*Homogyne alpina* (L.) Cass.	+	.	.
		***Piceetalia excelsae* Pawłowski et al., 1928 and *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al., 1939**			
P scap	Eurosiber.	*Picea abies* (L.) H.Karst.	2	3	1
P scap	Orof. Centroeurop.	*Larix decidua* Mill.	2	1	1
Ch frut	Circumbor.	*Vaccinium myrtillus* L.	+	1	1
NP	Circumbor.	*Juniperus communis* L.	.	2	1
Ch frut	Circumbor.	*Vaccinium vitis-idaea* L.	.	+	+
Ch rept	Orof. Eurasiat.	*Veronica officinalis* L.	+	+	.
H scap	Circumbor.	*Solidago virgaurea* L.	+	+	.
NP	Orof. S-Europ.	*Rosa pendulina* L.	.	1	.
H caesp	Orof. SW-Europ.	*Luzula nivea* (Nathh.) DC.	.	+	.
H scap	Europ.	*Laserpitium krapfii* Crantz subsp. *gaudinii* (Moretti) Thell.	.	+	.
		Other species			
H ros	Eurosiber.	*Alchemilla vulgaris* L. aggr.	.	+	+
H ros	Orof. SE-Europ.	*Aposeris foetida* (L.) Less.	.	+	+
H scap	Orof. S-Europ.	*Prunella grandiflora* (L.) Scholler	.	+	+
H scap	SE-Europ.	*Knautia drymeia* Heuff.	.	+	+
Ch frut	Orof. S-Europ.	*Erica carnea* L.	.	1	.
Ch suffr	Orof. S-Europ.	*Polygaloides chamaebuxus* (L.) O.Schwarz	.	+	.
P caesp	Circum-Artic-Alp.	*Alnus alnobetula* (Ehrh.) K.Koch	.	+	.
H rept	Cosmop.	*Fragaria vesca* L.	.	+	.
H scap	-	*Viola* spp.	.	+	.
H scap	Eurasiat.	*Polygala vulgaris* L.	.	.	+
H scap	Eurosiber.	*Hieracium murorum* L. aggr.	+	.	.

subalpine acidic pastures (*Nardion strictae*) with plants of nutrient-rich and moist mountain habitats of the classes *Molinio-Arrhenatheretea* Tx., 1937 and *Mulgedio-Aconitetea* Hadač & Klika in Klika & Hadač, 1944 (particularly in relevé 1, carried out on a flat surface), the community also includes shrubs of ecotonal/mantle communities dynamically connected to forests (*Crataego-Prunetea* Tx. 1962), as well as species of mature oro-boreal coniferous forests (*Piceion excelsae* and *Piceetalia excelsae* Pawłowski et al. 1928) (Table 1).

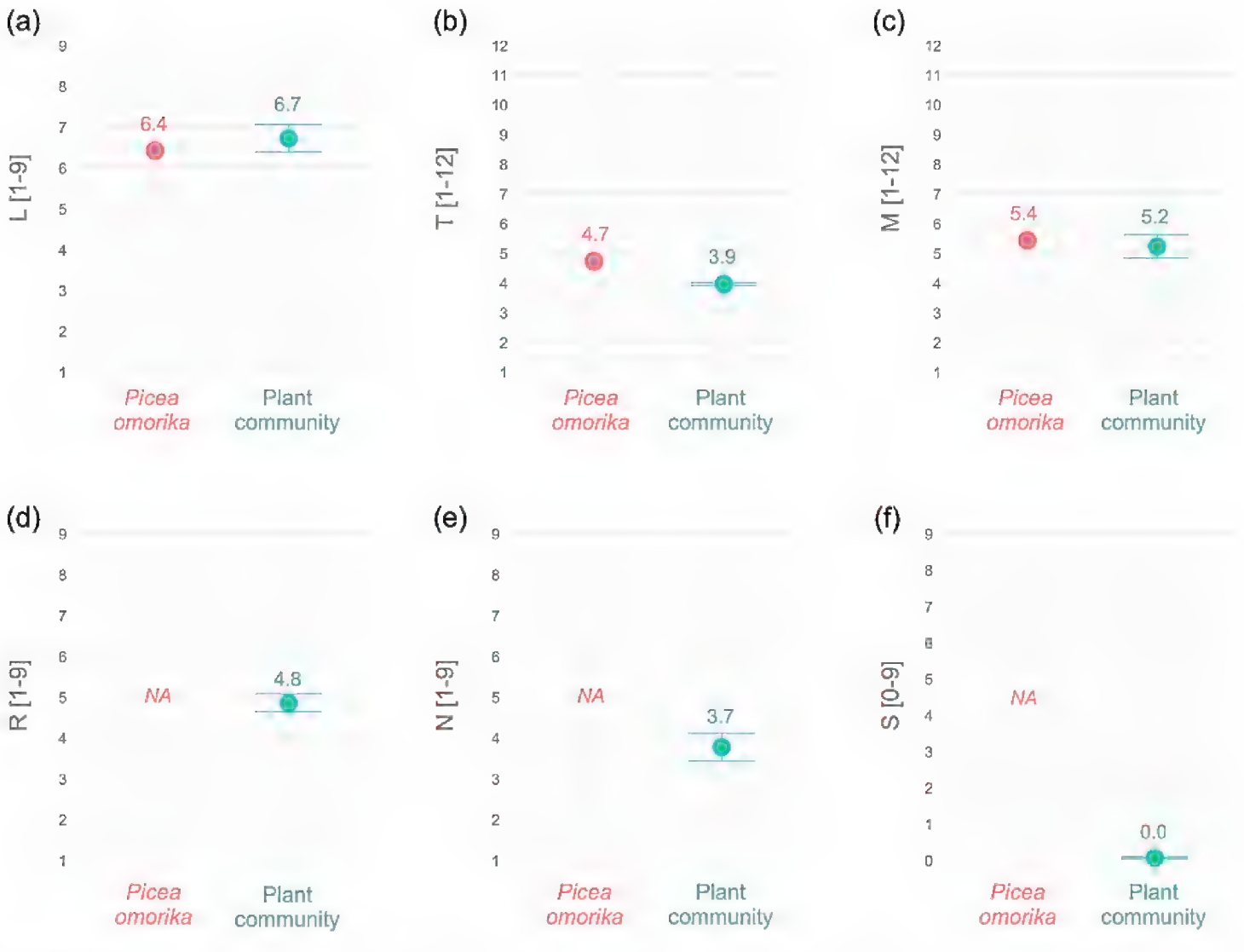

Figure 7. Comparison between the EIVs assigned to *Picea omorika* (Tichý et al. 2023) and those of the plant community in the study area. Key: L = light (**a**); T = temperature (**b**); M = moisture (**c**); R = reaction (**d**); N = nutrients (**e**); S = salinity (**f**); NA = not available data.

Fig. 7 shows the results of the application of EIVs. The *P. omorika* community is mainly composed of heliophilous species occurring in the high-mountain vegetational belt, on moderately moist, nutrient-poor, slightly acidic, and non-saline soils.

The comparison between the EIVs of the plant community in the study area and those assigned to *P. omorika*, based on the floristic-ecological features of the vegetation where it occurs in Serbia and Bosnia-Herzegovina, indicates that the mean M value of the community is similar to that of *P. omorika*, whereas the community values for the L and T indices are higher and lower than those of *P. omorika*, respectively.

Functional strategy

All 50 leaves analyzed for Grime's functional strategy showed the same values of C, S, and R (C = 0.0%, S = 100.0%, R = 0.0%), allowing *P. omorika* to be classified as a strictly stress-tolerant species. The triangular diagrams in Fig. 8 indicate that the *P. omorika* community is composed of species with different functional strategies, as they are distributed across the entire diagram except near the R vertex. Nevertheless, the community mean values and the kernel density distributions reveal a higher representation of stress-tolerant species, particularly when CSR values are weighted by species cover (Fig. 8b).

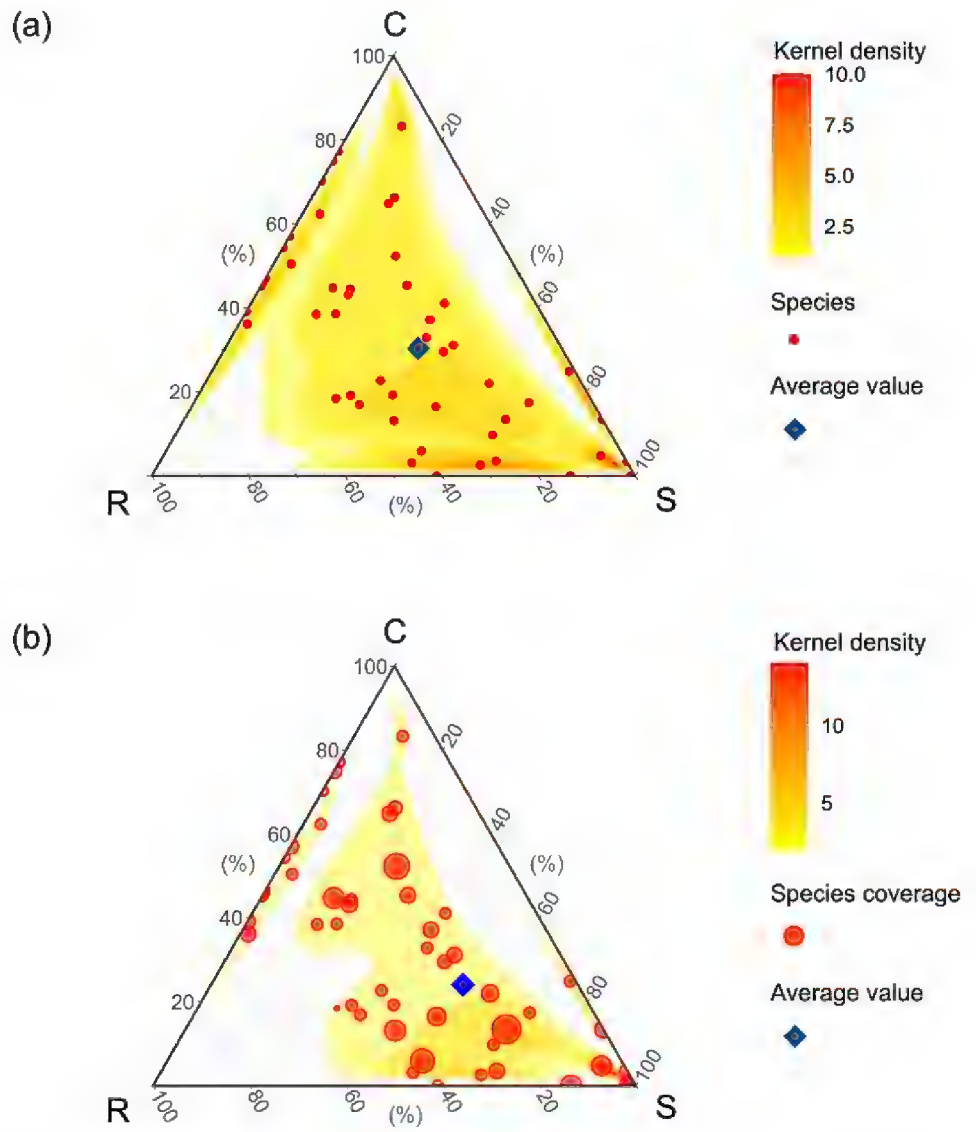

Figure 8. Species distribution within Grime's CSR ternary plot (C = competitor, S = stress-tolerant, R = ruderal): **a** kernel density of species positions (red circles), with the blue diamond indicating the average value **b** kernel density weighted by species coverage (circle size), with the blue diamond showing the average weighted value.

Discussion

Dendrochronological analysis revealed that the study area hosts *P. omorika* individuals of varying ages, including both young and mature trees (Fig. 6). This finding confirms that the stand is not the result of a forest plantation (which in the past typically consisted of even-aged individuals) but instead demonstrates the localised naturalisation of *P. omorika*. According to Richardson et al. (2000), naturalised species are alien plants that reproduce consistently and maintain self-sustaining populations over multiple generations without direct human intervention (or even despite it). In this case, naturalisation is restricted to a single hectare and originates from a single mother tree. *P. omorika*, therefore, represents a newly naturalised yet spatially restricted species contributing to the alien vascular flora of Italy, which currently comprises 1,782 taxa (Galasso et al. 2024).

Among the dated trees, the one located near the Armentarga hut was found to be considerably older than the others, suggesting that it was the first to produce viable seeds and initiate the species' establishment in the study area. Its presence near the hut for approximately 55–60 years makes it plausible that it was planted for ornamental purposes following the building's restoration, although current members of the "Penne

Nere" Alpine Group have no recollection of such an event (personal communication). It is, however, unlikely that *P. omorika* represents a glacial relict in this area, as no particularly old individuals were detected and the site was glaciated during the Würm glacial period (Ivy-Ochs 2015).

The absence of Serbian spruce individuals aged between 32 and 54 years (Fig. 6) may be attributed to a combination of ecological and physiological factors. From the late 1960s, when the first tree was likely planted near the Armentarga hut, until the mid-1990s, when *P. omorika* began reproducing, local climatic conditions may have been unfavourable for seed production or germination. Furthermore, this tree, which would have been approximately 25 years old in 1995, may not have reached reproductive maturity, as the species typically requires 20–30 years to produce fertile cones, according to experiments conducted at the Bedgebury National Pinetum (Kent, UK; Dallimore 1945).

Results show that the tree near the Armentarga hut has a CBH comparable to those of individuals roughly 20 years younger. The reduced radial growth of this tree may reflect less favourable climatic conditions during its first two decades, compared with those prevailing in subsequent years. Conversely, the group of *P. omorika* trees growing in the wood-pasture exhibits a nearly linear increase in CBH over time, indicative of stable and suitable environmental conditions (West 2024). These conditions correspond to a sub-oceanic climate, with moderately moist, nutrient-poor, and slightly acidic soils under cold, high-light conditions, as a result of the application of the EIVs (Fig. 7).

The synecological analysis also revealed differences between the EIVs assigned to *P. omorika* in Serbia and Bosnia-Herzegovina and the mean EIVs of the vegetation of the study area. Such discrepancies may help explain the ecological and conservation challenges affecting *P. omorika* in its native range, as well as contribute to a better definition of the species' fundamental niche. In the Brembana Valley, the species benefits from colder temperatures and open, well-lit habitats, conditions that differ markedly from the shaded forests it occupies in the Balkans, where it competes with several tree species such as beech (*Fagus sylvatica* L.) (Burschel 1965; Savill et al. 2017), a more thermophilous broadleaved species capable of forming dense, low-light stands. Beech is absent from the study area (Table 1) because, in the upper Brembana Valley, beech forests of *Fagetalia sylvaticae* Pawłowski, 1928 occur at lower elevations (800–1,500 m a.s.l.), whereas the high mountain and subalpine belts are characterised by open conifer forests dominated by spruce, larch, and Swiss stone pine (*Pinus cembra* L.; Del Favero 2002; Verde et al. 2010). The latter is a relict species in the south-Orobic District and, although absent from the relevés (Table 1), occurs near Lake Fregabolgia (Andreis et al. 2005; Martini et al. 2012).

Based on the results of this research, it is likely that the realised niche of *P. omorika* in its native range is strongly compressed by biotic competition relative to its fundamental niche, making standard Ellenberg ecological values potentially unrepresentative of the plant's actual eco-physiological capabilities. Therefore, it would be advisable to update the Ellenberg indicator values assigned to *P. omorika* by Tichý et al. (2023) in order to include the environmental characteristics of the Brembana Valley site.

Although the study area provides ecologically suitable conditions for *P. omorika*, the species does not currently display invasive behaviour, as it lacks the capacity for rapid spread or for generating negative impacts on native ecosystems (Richardson et al. 2000). Indeed, over the past three decades, only a few dozen individuals have established within a limited area. While these trees can create shaded microsites unsuitable for *Sanguisorba dodecandra* (similarly to *Picea abies* [L.] H.Karst.), they do not threaten the persistence of this endemic species of the Orobic Alps, which is widespread and abundant, often dominating pastures, meadows, avalanche tracks, and stream margins (Pirola 1964; Giupponi et al. 2022).

Although Richardson and Pyšek (2012) noted that all naturalised species possess potential invasiveness, *P. omorika* is unlikely to exhibit such behaviour due to its strongly stress-tolerant functional strategy. Dalle Fratte et al. (2019) showed that invasive alien plants in southern Europe typically display a CSR strategy with higher competitive (C) values than native species, suggesting that invasive plants in this biogeographic region are associated with relatively productive habitats. Consequently, native species inhabiting resource-poor environments are less likely to experience competitive pressure from aliens. In the present case, the habitat is characterised by low productivity due to nutrient limitation and low temperatures. Moreover, *P. omorika* competes primarily with *P. abies*, which shares the same CSR strategy (C = 0.0%, S = 100.0%, R = 0.0%), and with *Larix decidua* Mill., which, although slightly less stress-tolerant, remains predominantly S-strategist (C = 0.0%, S = 99.2%, R = 0.8%) (Pierce et al. 2017).

The functional CSR strategy of *P. omorika* also suggests that this species becomes part of the plant communities in mature forests. Indeed, according to Grime (2001), the final stages of plant succession (whether primary or secondary) are characterised by the predominance of stress-tolerant species. In this study, the plant community of *P. omorika* was composed of species with different strategies, although most were stress-tolerant (Fig. 8). This pattern is explained by the ongoing secondary succession in the study area, which involves the gradual replacement of *Nardion strictae* pastures with meadow species (*Molinio-Arrhenatheretea*) and megaphorb species of *Mulgedio-Aconitetea* (initial stage with some competitive species), leading to the high-montane coniferous forest of *Picea excelsae* (final stage). Intermediate stages, based on the interpretation of phytosociological data, may include the *Rubetum idaei* Kaiser, 1926 association, dominated by *Rubus idaeus* L. subsp. *idaeus*, which in the Alps develops following the abandonment of mountain pastures or in Norway spruce forests affected by disturbance events (Verde et al. 2010; Giupponi et al. 2023, 2025).

Similar examples of rare or narrowly endemic coniferous species occurring outside their native ranges include *Pinus radiata* D.Don (Monterey pine), a species native to a limited coastal region of California that has been widely planted outside its native range for forestry and ornamental purposes. In New Zealand, *P. radiata* has become naturalised from plantation sources, invading grasslands, shrublands, and some forested areas, with climate-niche modelling indicating that large portions of the country are climatically suitable for its spread beyond plantation sites, highlighting its potential ecological impact (Bellingham et al. 2023). Similar patterns of spread and naturalisation from

plantations have been documented in Chile and South Africa, where *P. radiata* escapes from planted forests and can modify native ecosystems (Calviño-Cancela and van Etten 2018). *Pinus radiata* is also an alien species in Italy, where it is naturalised in the Sardinia administrative region (Galasso et al. 2023). This case demonstrates that even tree species with restricted native distributions can establish self-sustaining populations outside their native ranges under suitable ecological conditions, and that their introduction may cause alterations to ecosystems, suggesting that particular caution should be exercised regarding the spread of exotic species, even within conservation-oriented actions aimed at rare or threatened species (e.g. translocations).

Future studies focusing on vegetation dynamics in the study area would be valuable to determine whether and how *Picea omorika* might influence the floristic and physiognomic features of intermediate and mature successional stages. In particular, it would be useful to define the syntaxonomic framework of the mature forest that *P. omorika* may form in Brembana Valley. Phytosociological analysis (Table 1) suggests that *P. omorika* may establish within forest communities of *Piceion excelsae* (*Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939), which are very different from those of *Erico carneae-Piceion omorikae* (*Erico-Pinetea* Horvat, 1959) communities described in Serbia and Bosnia-Herzegovina (Mucina et al. 2016). Additionally, species distribution models (SDMs) could be applied to predict the potential expansion of *P. omorika*, helping to identify suitable habitats based on climatic and edaphic factors influencing both the species' native range and the Brembana Valley site. These tools are increasingly accurate and widely used to assess species' ecological niches and their potential distribution, including in the Alps (Pedrali et al. 2024; Giupponi et al. 2025).

Gaining a better understanding of the ecological role and effects of *P. omorika* on the ecosystems of the Brembana Valley is important, including its potential impacts on soil chemistry, such as acidification. Monitoring its spread and any potential competition with *P. abies* (or other species) is also necessary, particularly because the study area lies within the Orobie Bergamasche Regional Park, a protected area of high natural value and rich in endemic species (Andreis et al. 2017; Giupponi and Giorgi 2017, 2019). Such knowledge would support land managers in making scientifically informed decisions regarding nature conservation actions, including eradication. In this specific case, given that *P. omorika* is an endangered species and currently shows low invasive potential, its eradication in the Brembana Valley should be avoided, unless evidence of invasive behaviour emerges under ongoing climate change. Conversely, the study area could be considered for carefully evaluated translocation efforts aimed at preserving the species without causing significant alterations to the ecosystem. Although translocation could represent a strategy to safeguard *P. omorika*, conservation actions should primarily focus on measures conducted within its native range, such as conservation in botanical gardens, greenhouses and/or nurseries. These conservation strategies have been successfully applied to other endangered conifers, such as *Abies nebrodensis* (Lojac.) Mattei in Sicily (Benelli et al. 2024), where seed collection, cultivation of seedlings, and maintenance of clonal orchards in botanical gardens and arboreta have helped preserve genetic diversity.

Conclusions

This study reports the first documented case of localised naturalisation of *P. omorika* in Italy and, more broadly, in an area outside Serbia and Bosnia-Herzegovina, thereby adding the species to the alien vascular flora of Italy.

Stand-age analysis indicated that this population likely originated from the planting of a Serbian spruce near the Armentarga hut in the late 1960s for ornamental purposes. Environmental conditions in the study area over the past decades have proven favourable for *P. omorika*, allowing the development of an uneven-aged population of approximately 50–60 individuals within a pasture of *Nardion strictae*. Here, an active secondary succession is currently underway, which is expected to lead to the formation of a high-montane coniferous forest of *Piceion excelsae*. In addition to the sub-oceanic pre-Alpine climatic context, Serbian spruces in the upper Brembana Valley grow on moderately moist, nutrient-poor, and slightly acidic soils, under cold and high-light conditions, as inferred from the application of the EIVs. The stress-tolerant strategy of *P. omorika* supports its ability to grow in cold environments with nutrient-poor soils, and also suggests a low invasive potential.

The open woodland structure (wood pasture) and the low temperatures typical of the high-montane vegetation belt are the two ecological factors that most distinguish the *P. omorika* community in the Brembana Valley from those in its native range in Serbia and Bosnia-Herzegovina. These findings contribute to a better definition of the species' fundamental niche, further elucidating the range of climatic and edaphic conditions under which *P. omorika* can survive and reproduce.

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